Do exotic earthworms invade New Zealand native forests?

Nicole L. Schon[1]*, S. Bartlam[2], E. L. Deakin[2,3], R.A. Gray[4], A. D. Mackay[4], C. van Koten[1]

[1] AgResearch, Lincoln, Private Bag 4749, Christchurch 8140, New Zealand
[2] Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand
[3] University of Canterbury, School of Biological Sciences, Private Bag 4800, Christchurch, New Zealand
[4] AgResearch, Grasslands, Private Bag 11008, Palmerston North 4442, New Zealand
* Corresponding author: Nicole.Schon@agresearch.co.nz

(Received October 2016, revised and accepted December 2016)

Abstract

New Zealand forest soils contain a rich diversity of native earthworm species, while our pasture soils are dominated by exotic earthworms which were unintentionally introduced in the 19th century. In North America, the invasion of exotic earthworms into what was previously earthworm free forest is causing considerable ecosystem changes. The aims of this study were to determine whether exotic earthworms were present in native forest remnants adjacent to pasture soils and determine the implications of this on the native earthworm populations. Four forest remnants and a reserve adjacent to agricultural pastures were sampled in the Waikato, New Zealand. Forest-pasture transects were sampled and analysed for earthworms. There existed a clear distinction in the species composition of the earthworm communities at our sites, with exotic earthworms almost exclusively in pasture soils and native earthworms in forest soils. The presence of exotic earthworms in the forest was rare, with no earthworms detected 3 m into the forest, and only a few being detected 9 m downslope into the forest. Our results suggest exotic earthworms found in the forest represent only sporadic migration of earthworms.

Keywords: Earthworms, exotic species, forest remnants, invasions, pasture, soil

Introduction

There have been a large number of exotic plant and animal species introduced into New Zealand that have had a large impact on our native ecosystems (Allen & Lee, 2006). The invasion of exotic invertebrates appear to have less of an impact (Brockerhoff et al., 2010). However, there have been few studies which have explored the potential of exotic earthworms to invade our forest soils (Lee, 1961, Springett et al., 1998). Exotic earthworms arrived in New Zealand accidentally with the European settlers in the 19th century (Stockdill, 1982). These exotic earthworms are beneficial to agriculture, playing a critical role in organic matter decomposition, nutrient cycling and maintenance of soil structure (Edwards & Bohlen, 1996). Native forests bound our pasture systems, with numerous small native forest remnants embedded in New Zealand pastoral landscapes (Didham et al., 2009). There is increasing recognition of the conservation value of forest remnants and growing interest in their protection (Melo et al., 2013).

Evidence from North America suggests that exotic earthworms can have large effects on the forest soil ecosystem (Bohlen et al., 2004, Eisenhauer et al., 2007). The invasion of exotic earthworms into North American forests has caused the rapid incorporation of the forest litter layer, lowering soil carbon (Bohlen et al., 2004, Eisenhauer et al., 2007) and increasing the soils bulk density, and ultimately altering the forest understory (Eisenhauer et al., 2007, Hale et al., 2005). Exotic earthworms in New Zealand have a patchy distribution (Schon et al., 2011a, Springett, 1992). An estimated 6.5 million ha of pastures in New Zealand would potentially benefit from the introduction of anecics (Schon et al., 2011a), an earthworm functional group that burrows deep into the soil profile (Paoletti et al., 1991). We need to ensure that their benefits to our pasture systems do not come at the cost of our native forest systems. The aim of this study was to determine whether exotic earthworms were present in native forest remnants adjacent to pasture soils and determine the implications of this on the native earthworm populations.

Materials and methods

Study sites

Four forest remnants adjacent to agricultural pastures were sampled near Te Miro in the Waikato region, New Zealand as part of a larger study (Didham et al., 2015). Remnants ranged in size from 3 to 16 ha, with a forest reserve of 409 ha also sampled (Table 1). Pastures were grazed by either sheep and cattle or dairy cattle. Livestock were excluded from the majority of the remnants via fencing protection for a minimum of 10 years, but one unfenced remnant was also sampled. All forest remnants were situated downslope of the pasture. The tawa-dominated (*Beilschmiedia tawa*) remnants (Didham et al., 2009) had been regenerating for less than 25 years and were previously assessed for soil properties, soil, litter and aboveground invertebrate communities, litter decomposition and herbage composition (Deakin, 2013). Earthworms had not been previously assessed at these sites, however, exotic earthworms in pasture were known to be abundant within the region (Schon et al., 2011b, Schon et al., 2008).

Soil samples (20 cm width x 20 cm length x 30 cm depth) were collected

Table 1. Size of forest remnants and their soil types.

Site	Size (ha)	Fenced	Lattitutude Longitude	Soil series	Soil order
1	3	Fenced	37.8709 175.6360	Pukerata silt loam hill	Brown
2	4	Unfenced	37.7942 175.5181	Tauwhare sandy loam hill	Recent
3	4	Fenced	37.8327 175.5783	Otorohanga silt loam	Allophanic
4	16	Fenced	37.8342 175.5575	Pukerata silt loam hill	Brown
Reserve	409	Fenced	37.7945 175.5265	Pukerata silt loam hill	Brown

using a spade along a log-scale transect at 3, 9 and 27 m downslope into the native forest fragment and 9 and 46 m upslope into the pasture. We also collected samples at the forest-pasture edge (designated 0 m). At each distance three monoliths were sampled. The soil was hand-sorted for earthworms, which were identified to species where possible (Schon et al., 2014). Due to the size of the monoliths and nature of extraction many of the larger native earthworms were not identified as whole specimens were not collected (e.g. Spenceriella gigantea can reach 1.4 m in length).

Soil chemical and physical properties were collected at the pasture (3 and 46.5 m), edge (0 m) and forest (3, 9 and 27 m). Three replicate samples, a composite of 6 cores (20 mm in diameter, 100 mm depth), were collected for pH (1:2.5 soil to water ratio), Olsen phosphorus (P) (Olsen et al., 1954), and total C and N (LECO, TruSpec, St Joseph, MI, USA). Total P was analysed by inductively coupled plasma—mass spectrometry (ICP-MS) (Martin et al., 1994). Values were corrected for soil moisture factor and bulk density. Three replicate intact samples were taken for bulk density, using 98 mm diameter, 75 mm depth steel rings, which were weighed moist, oven-dried at 105°C and re-weighed to three decimal places. Bulk density was not assessed at site 3. Soil was passed through a 6 mm sieve and air dried before analysis. Litter, loose organic matter, grass, and grass roots were removed from the top of the cores, making their effective depth range approximately 10-100 mm.

Statistical analysis was conducted using a generalised linear modelling (GLM) approach assuming group-specific negative binomial distributions through a log link function. The GLM analysis was applied to total abundances of exotic and native earthworms (i.e. two independent GLM analyses - one to exotic earthworm abundance, and the other for native earthworm abundance). Each of the exotic earthworm species was also analysed separately. Each GLM analysis initially considered three factors: (1) location (pasture, edge, forest), (2) distance and (3) site. However, the latter two factors were not statistically significant, and were therefore removed from the final analysis. This paper presents results for an initial analysis with the three factors and a subsequent analysis with only the location factor. All of the above analyses were carried out using statistical software SAS version 9.3.

Results

Soil bulk density, total N and total P were higher in grazed pasture soils than in the forest soils (Table 2). There was no significant influence of pasture or forest

Table 2. Soil properties of the sampled transects (0-10 cm) as an average across all sites. Pasture average of 3 and 46 m, forest average of 3, 9 and 27 m. * Soil analysis at Site 3 measured for 0-7.5cm depth, with a total soil C of 14.9% and a total soil N of 1.1%.

Location	Bulk density (g/cm^3)	pH	Total C (mg/cm^3)	Total N (mg/cm^3)	C:N ratio	Olsen P (ug/cm^3)	Total P (ug/cm^3)
Pasture	0.66b	*5.39*	57.65	5.97b	9.7	7.3	742.3b
Edge	0.55ab	*5.37*	46.54	4.51a	10.5	5.3	484.1a
Forest	0.55a	*5.36*	48.34	4.54a	10.7	4.8	429.3a

on soil pH, total C and C:N ratio.

A total of 874 exotic and 14 native earthworms were identified in this study. Native earthworm abundance was much lower than the exotic earthworms (Table 3). Although native earthworm species were more abundant in forest compared to pasture soils (P=0.006), this was only significant at site 4 (P=0.04). Despite this, native earthworms were detected in at least one of the sampling points in the forest remnants at each site. A total of seven native species were observed, the most abundant was *Megascolecidae sp.*3 found at 33 m^{-2}, and the most common was *Megascolecidae sp.* 2 found at three sites. No native earthworms were detected in the pasture soil, but one native earthworm was detected on the forest edge at site 1.

The exotic earthworm species *Aporrectodea caliginosa*, *Lumbricus rubellus* and *Octolasion cyaneum* were detected in the pasture at all sites (Table 3, Appendix 1). Two other exotic species, *Aporrectodea longa* and *Lumbricus terrestris* were only detected at two separate sites. Exotic earthworm abundance was higher in the pasture than at the forest edge (P<0.0001) and within the forest (P<0.0001).

At all sites, pasture areas had a significantly higher abundance of *A. caliginosa* (P<0.0001) and *L. rubellus* (P<0.0001) than forest remnants, with their abundance higher at the forest edge than in the forest remnants (P<0.0001 for both). Pastures had a higher abundance of *O. cyaneum* than the adjacent forest areas (P=0.003), particularly in the reserve and sites 2 and 4. In two fenced sites (sites 1 and 3), two individuals of *O. cyaneum* and one individual of *A. caliginosa* were

Table 3. Average earthworm species abundance (ind./m^2) across all sites at each location (pasture, edge and forest, n=30, 15 and 45, respectively).

Location	Exotic earthworm species					Total exotics	Total Natives
	cali	*rub*	*cyan*	*long*	*terr*		
Pasture	305^a	*96^a*	24^a	14^a	2	441^a	0^a
Edge	25^b	*13^b*	7^{ab}	0^b	0	45^b	2^{ab}
Forest	1^c	*0^c*	1^b	0^b	0	2^c	7^b

^{a}, ^{b}, ^{c} indicate significant difference at α=0.05 in a given column.
Exotic earthworm species: cali - *Aporrectodea caliginosa* (Savigny, 1826), rub - *Lumbricus rubellus* (Hoffmeister, 1843), cyan - *Octolasion cyaneum* (Savigny, 1826), long - *Aporrectodea longa* (Ude, 1885), terr - *Lumbricus terrestris* (Linnaeus, 1758).
Native earthworm species include: *Oligochaeta sp.* 1, *Megascolecidae sp.* 1, *Megascolecidae sp.*2, *Megascolides raglani* (Lee, 1952), *Megascolecidae sp.*3, *Maoridrilus plumbeus* (Beddard, 1895), *Megascolecidae sp.* 4.

detected at a distance of 9 m into the forest. *Aporrectodea longa* was more abundant in the pasture than in the forest soil (P=0.002), at site 3 where it was detected. A low abundance of *L. terrestris* was also detected under pasture at a single site (site 4), but was not different from 0. There was no significant difference in total abundance of exotic earthworms at 9 m in comparison to 46.5 m into the pasture.

Discussion

There existed a clear distinction in the species composition of the earthworm communities at our sites, with exotic earthworms almost exclusively in pasture soils and native earthworms only in forest soils. The abundance of native earthworms was lower than the exotic earthworms, but typical of New Zealand conditions (Springett, 1992, Bartlam, pers. comm.). This preference of exotic earthworms for pasture soils, and natives for forest soils has also been observed by Dalby et al., (1998) in Australia.

Three individual exotic earthworms (one *A. caliginosa* and two *O. cyaneum*) were detected 9 m inside the forest at two sites. There were, however, no exotic earthworms detected 3 m into the forest, indicating that there was no invasion front moving into the forest. Because these remnants were situated downslope of the pasture it is possible that the earthworms were washed into the forest during a heavy rainfall event. Sporadic movement into the forest does not necessarily result in the establishment of exotic earthworms in the forest. Lee (1961) and S. Bartlam (pers. comm.) also found little evidence of exotic earthworms in New Zealand forest soils.

It is expected that this distinction in earthworms between the forest and pasture soils reflects differences in the soil physical and chemical properties (Hendrix et al., 2006, Lee, 1961, Marichal et al., 2012). At our study sites, the forest soils were less compacted and had a lower fertility (total N and total P). The lower quality litter and distinct microbial communities present in forest soils (Dickinson et al., 1981) are likely to favour the feeding preferences of New Zealand's native earthworms. Native earthworm species are highly specialised and adapted to specific forest conditions, giving rise to the high species diversity (Lee, 1961). However, Kim et al., (2015) observed both native and exotic earthworms to prefer agricultural soil in choice chamber experiments. This may explain that although native earthworms are typically absent from pasture soils, in some low fertility pastures (where the physical disturbances are minimised) native earthworms, such as the subsoil dwelling *Octochaetus multiporous* has higher abundances (200 ind. m^2) compared to both high fertility pastures and native forests (20 ind. m^2) (Springett et al., 1998).

The invasion of exotic earthworms, such as *L. terrestris*, into North American forests show, that despite a preference for pasture soils there is potential for exotic earthworms to migrate into forests. This migration may also occur in New Zealand given more time as earthworm dispersal is slow (Hendrix et al., 2006), and the abundance of *L. terrestris*, for example, is still low and their distribution localised (detected at one site in this study). In North America, where earthworms arrived a hundred years earlier than in New Zealand, forests remained free of earthworms until 1985 (Eisenhauer et al., 2007). In Europe, earthworms are also migrating, with the migrating earthworms feeding on different sources of organic matter, potentially altering carbon and nitrogen dynamics (Melody & Schmidt, 2012).

Although there was no evidence of exotic earthworms migrating into forest fragments, there is still potential for this to occur in New Zealand.

The impact of a potential invasion of exotic earthworms into New Zealand forests may be minimised because of the differing dynamics between New Zealand evergreen forests and North American deciduous forests. One of the most important contributing factors may be that New Zealand has existing populations of native earthworms, while North America does not (Eisenhauer et al., 2007). The presence of native earthworm species appears to limit the impact of exotic earthworms (Hendrix et al., 2006). New Zealand has a rich diversity of native earthworm species, with 177 native species already described (Buckley, 2015), this includes both topsoil and subsoil dwelling species (Lee, 1961). These species occupy the same functional groups as seen in our exotic earthworms. While little is known about their feeding preferences, the relatively high number of species occupying a range of habitats may limit the ability for exotic earthworms to migrate into forests, while also limiting the potential impact of exotic earthworms on the forest ecosystem. Lee (1961) observed no competition between exotic and native earthworms in New Zealand pastures that had been converted from native forests, and noted that in undisturbed, temperate, evergreen forests exotic earthworms were usually absent.

In summary, the presence of exotic earthworms in forest remnants in the Waikato region, New Zealand remains rare. The introduction of exotic earthworms to pasture soils to benefit pasture production may be possible without the detriment to our native remnants. However, the potential exists for them to migrate into forests, despite appearing to have a strong preference for agricultural soils. Since earthworm migration into forests may occur over longer time periods and the current study was limited to one region in New Zealand, further investigation to confirm that exotic earthworms prefer agricultural soils in other regions is warranted. Investigation should be extended to include other natural ecosystems and potential for human dispersal into these systems.

Acknowledgements

We would like thank the landowners for permission to sample on their properties, L. Fisk and H. Wright for the soil analysis, and C. van Koten for the statistical analysis. We are grateful for funding received from the New Zealand Agriculture Greenhouse Gas Research Centre.

References

Allen, R.B. & Lee, W.G. 2006. Biological Invasions in New Zealand. Springer, Berlin. 457 pp.

Bohlen, P.J., Pelletier, D.M., Groffman, P.M., Fahey, T.J. & Fisk, M.C. 2004. Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests. *Ecosystems*: 7, 13-27.

Brockerhoff, E.G., Barratt, B.I.P., Beggs, J.R., Fagan, L.L., Kay, M.K., Phillips, C.B.& Vink, C.J. 2010. Impacts of exotic invertebrates on New Zealand's indigenous species and ecosystems. *New Zealand Journal of Ecology*: 34, 158-174.

Buckley, T.R., Boyer, S., Bartlam, S., Hitchmough, R., Rolfe, J., Stringer, I., 2015. Conservation status of New Zealand earthworms, 2014. Department of Conservation,

Wellington, New Zealand.
Dalby, P.R., Baker, G.H. & Smith, S.E. 1998. Potential impact of an introduced lumbricid on a native woodland in South Australia. *Applied Soil Ecology*: 9, 351-354.
Deakin, E.L., 2013. Impacts of land-use intensification on forest remnants embedded within production landscapes. A thesis presented in partial fulfilment of the requirements of the degree for the Doctor of Philosophy in Biological Sciences at University of Canterbury, Canterbury, New Zealand.
Dickinson, C.H., Underhay, V.S.H. & Ross, V. 1981. Effect of season, soil fauna and water content on the decomposition of cattle dung pats. *New Phytologist*: 88, 129-141.
Didham, R.K., Barker, G.M., Bartlam, S., Deakin, E.L., Denmead, L.H., Fisk, L.M., Peters, J.M., Tylianakis, J.M., Wright, H.R. & Schipper, L.A. 2015. Agricultural intensification exacerbates spillover effects on soil biogeochemistry in adjacent forest remnants. *Plos One*: 10, e0116474.
Didham, R.K., Barker, G.M., Costall, J.A., Denmead, L.H., Floyd, C.G. & Watts, C.H. 2009. The interactive effects of livestock exclusion and mammalian pest control on the restoration of invertebrate communities in small forest remnants. *New Zealand Journal of Zoology*: 36, 135-163.
Edwards, C.A. & Bohlen, P.J. 1996. Biology and Ecology of Earthworms. Chapman & Hall, London, UK. 426 pp.
Eisenhauer, N., Partsch, S., Parkinson, D.& Scheu, S. 2007. Invasion of a deciduous forest by earthworms: Changes in soil chemistry, microflora, microarthropods and vegetation. *Soil Biology and Biochemistry*: 39, 1099-1110.
Hale, C.M., Frelich, L.E., Reich, P.B. & Pastor, J. 2005. Effects of European earthworm invasion on soil characteristics in Northern Hardwood Forests of Minnesota, USA. *Ecosystems*: 8, 911-927.
Hendrix, P.F., Baker, G.H., Callaham Jr, M.A., Damoff, G.A., Fragoso, C., González, G., James, S.W., Lachnicht, S.L., Winsome, T. & Zou, X. 2006. Invasion of exotic earthworms into ecosystems inhabited by native earthworms. *Biological Invasions*: 8, 1287-1300.
Kim, Y.-K., Robinson, B., Boyer, S., Zhong, H.-Y.& Dickinson, N. 2015. Interactions of native and introduced earthworms with soils and plant rhizospheres in production landscapes of New Zealand. *Applied Soil Ecology*: 96, 141-150.
Lee, K.E. 1961. Interactions between native and introduced earthworms. *New Zealand Journal of Ecology*: 8, 60-62.
Marichal, R., Grimaldi, M., Mathieu, J., Brown, G.G., Desjardins, T., Silva Junior, M.L.d., Praxedes, C., Martins, M.B., Velasquez, E.& Lavelle, P. 2012. Is invasion of deforested Amazonia by the earthworm Pontoscolex corethrurus driven by soil texture and chemical properties? *Pedobiologia*: 55, 233-240.
Martin, T.D., Creed, J.T. & Brockhoff, C.A. 1994. Method 200.2: Sample preparation procedure for spectrochemical determination for total recoverable elements. Revision 2.8, EMMC version. Cincinnati, Ohio, USA: U.S. Environmental Protection Agency.
Melo, F.P.L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M. & Tabarelli, M. 2013. On the hope

for biodiversity-friendly tropical landscapes. *Trends in Ecology and Evolution*: 1649, 1-7.

Melody, C. & Schmidt, O. 2012. Northward range extension of an endemic soil decomposer with a distinct trophic position. *Biology Letters*: doi:10.1098/rsbl.2012.0537 1744-1957X

Olsen, S.R., Cole, C.V., Wanatabe, F.S. & Dean, L.A. 1954. Estimation of available phosphorus in soils by extraction with sodium hydrogen carbonate. In: U.S.D.A. Circ. 939

Paoletti, M.G., Favretto, M.R., Stinner, B.R., Purrington, F.F. & Bater, J.E. 1991. Invertebrates as bioindicators of soil use. *Agriculture, Ecosystems & Environment*: 34, 341-362.

Schon, N.L., Mackay, A.D., Gray, R.A. & Dodd, M.B. 2014. The action of an anecic earthworm (*Aporrectodea longa*) on vertical soil carbon distribution in New Zealand pastures several decades after their introduction. *European Journal of Soil Biology*: 62, 101-104.

Schon, N.L., Mackay, A.D. & Minor, M.A. 2011a. Earthworms in New Zealand sheep- and dairy-grazed pastures with focus on anecic Aporrectodea longa. *Pedobiologia*: 54, S131-137.

Schon, N.L., Mackay, A.D. & Minor, M.A. 2011b. Effects of dairy cow treading pressures and food resources on invertebrates in two contrasting and co-occurring soils. *Soil Research*: 49, 703-714.

Schon, N.L., Mackay, A.D., Minor, M.A., Yeates, G.W. & Hedley, M.J. 2008. Soil fauna in grazed New Zealand hill country pastures at two management intensities. *Applied Soil Ecology*: 40, 218-228.

Springett, J.A. 1992. Distribution of lumbricid earthworms in New Zealand. *Soil Biology and Biochemistry*: 24, 1377-1381.

Springett, J.A., Gray, R.A.J., Barker, D.J., Lambert, M.G., Mackay, A.D.& Thomas, V.J. 1998. Population density and distribution of the New Zealand indigenous earthworm Octochaetus multiporus (*Megascolecidae* : *Oligochaeta*) in hill pastures. *New Zealand Journal of Ecology*: 22, 87-93.

Stockdill, S.M.J. 1982. Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia*: 24, 281-299.

Appendix

Appendix 1. Locations and abundances of earthworm species observed in this study.

Site	Distance (m)	Location	Exotic earthworm species					Total exotics	Total natives
			cali	*rub*	*cyan*	*long*	*terr*		
Average		Pasture	305^{a}	96^{a}	24^{a}	14^{a}	2	441^{a}	0^{a}
		Edge	25^{b}	13^{b}	7^{ab}	0^{b}	0	45^{b}	2^{ab}
		Forest	1^{c}	0^{c}	1^{b}	0^{b}	0	2^{c}	7^{b}
1	46	Pasture	208^{a}	50^{a}	0^{a}	0	0	258^{a}	0^{a}
	9	Pasture	133^{a}	92^{a}	17^{b}	0	0	242^{a}	0^{a}
	0	Edge	8^{b}	0^{b}	0^{a}	0	0	8^{b}	8$^{b,\#}$
	3	Forest	0^{c}	0^{b}	0^{a}	0	0	0^{c}	0^{a}
	9	Forest	8^{b}	0^{b}	8^{a}	0	0	16^{b}	0^{a}
	27	Forest	0^{c}	0^{b}	0^{a}	0	0	0^{b}	8^{b,*}
2	46	Pasture	433^{a}	142^{a}	25^{a}	0	0	600^{a}	0^{a}
	9	Pasture	50^{b}	92^{a}	58^{a}	0	0	200^{ab}	0^{a}
	0	Edge	42^{b}	50^{a}	8^{ab}	0	0	100^{b}	0^{a}
	3	Forest	0^{b}	0^{b}	0^{b}	0	0	0^{c}	0^{a}
	9	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	8^{b,†}
	27	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	0^{a}
3	46	Pasture	375^{a}	50^{a}	0^{a}	67^{a}	0	492^{a}	0^{a}
	9	Pasture	150^{a}	25^{a}	17^{b}	75^{a}	0	267^{a}	0^{a}
	0	Edge	0^{b}	0^{b}	0^{a}	0^{b}	0	0^{b}	0^{a}
	3	Forest	0^{b}	0^{b}	0^{a}	0^{b}	0	0^{b}	0^{a}
	9	Forest	0^{b}	0^{b}	8^{ab}	0^{b}	0	8^{c}	17^{b,†}
	27	Forest	0^{b}	0^{b}	0^{a}	0^{b}	0	0^{b}	0^{a}
4	46	Pasture	558^{a}	233^{a}	25^{a}	0	17	833^{a}	0^{a}
	9	Pasture	233^{ab}	150^{a}	42^{a}	0	0	425^{a}	0^{a}
	0	Edge	58^{b}	0^{b}	8^{ab}	0	0	66^{b}	0^{a}
	3	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	0^{a}
	9	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	8^{b,‡}
	27	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	33$^{b,\#\#}$
Reserve	46	Pasture	442^{a}	42^{a}	50^{a}	0	0	534^{a}	0^{a}
	9	Pasture	467^{a}	83^{a}	8^{ab}	0	0	558^{a}	0^{a}
	0	Edge	17^{b}	17^{a}	17^{a}	0	0	51^{b}	0^{a}
	3	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	8^{b,**}
	9	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	8^{b,†}
	27	Forest	0^{c}	0^{b}	0^{b}	0	0	0^{c}	8^{b,††}

$^{a, b, c}$ indicate significant difference at $\alpha=0.05$ in a given column.
Exotic earthworm species: cali - *Aporrectodea caliginosa* (Savigny, 1826), rub - *Lumbricus rubellus* (Hoffmeister, 1843), cyan - *Octolasion cyaneum* (Savigny, 1826), long - *Aporrectodea longa* (Ude, 1885), terr - *Lumbricus terrestris* (Linnaeus, 1758).
Native earthworm species: ($^{\#}$) *Oligochaeta sp.* 1, (*) *Megascolecidae sp.* 1, (†) *Megascolecidae sp.*2, (‡) *Megascolides raglani* (Lee 1952), ($^{\#\#}$) *Megascolecidae sp.*3, (**) *Maoridrilus plumbeus* (Beddard 1895), (††) *Megascolecidae sp.* 4.